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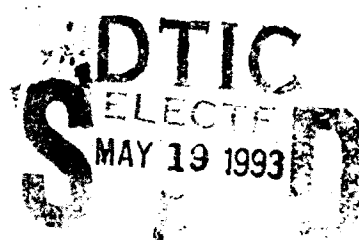


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A Simple Computational Model of Center-Surround Receptive Fields in the Retina

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A Simple Computational Model of Center-Surround Receptive Fields in the Retina

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BACKGROUND

Mead and Mahowald (1988) presented a silicon implementation of the outer layers of the vertebrate retina that produced center-surround receptive fields by simple processes of spatiotemporal integration and differencing. In the present paper, we offer a simple computational model of the outer retinal layers similar to that of Mead and Mahowald (1988). The current algorithm incorporates, in addition to center-surround receptive fields, both rectified on-center/off-surround and off-center/on-surround bipolar elements, and an increase in the convergence of receptors to output elements with eccentricity that accounts for resolution differences between central and peripheral vision. The phenomenon of even and odd symmetry that is observed in biological receptive fields can be reproduced by the response of the model system to a moving line.

RECEPTIVE FIELDS

The output cells of the biological retina respond differentially to contrast in a localized region of the receptor surface. A small bright spot will evoke a vigorous response in some cells, called on-center cells, and depress these same cells when the spot is moved somewhat away from their center into an annular surround. This region of depression is called an off-surround for the on-center cells (Kuffler and Nicholls, 1976). Off-center/on-surround cells have opposite characteristics in response to light.

Rodieck (1965) noted that the receptive fields of the retinal ganglion cells could be described by a difference of Gaussians (DoG). In Cartesian coordinates, with origin at the center of the receptive field, the response of such a cell may be written as

$$G_1(x,y) - G_2(x,y) = \\ K_1 * \exp(-(x^2+y^2)/\sigma_1^2) - K_2 * \exp(-(x^2+y^2)/\sigma_2^2),$$

where $K_1 > K_2$ and $\sigma_2 > \sigma_1$.

The first Gaussian accounts for the center sensitivity and the second Gaussian accounts for the surround sensitivity.

The silicon retina of Mead and Mahowald (1988) demonstrated that the center-surround receptive fields could be achieved directly by using simple additions and subtractions of time variant potentials. The heart of their model was a hexagonal matrix of resistors that served as analogues of the retinal horizontal cells to spatially and temporally average receptor potentials. An output amplifier took the difference between the current receptor potential and the local representation of the history of receptor potentials in the neighborhood. Their simple algorithm may more closely represent the mechanisms of the neural computation than do the descriptive abstractions of the DoG.

While the model of Mead and Mahowald (1988) successfully emulated processing in the outer layers of the biological retina, several additional architectural details and mechanisms can be implemented to improve the emulation of retinal functions. These include complementary center-surround receptive fields, and an increase in receptive field size coupled with an increase in receptive field center spacing with eccentricity (distance from the center of the receptor surface).

The receptive fields of the retinal ganglion output cells are spatial integrations of one or more receptors, and show considerable overlap of their dendritic arborizations that collect input (Wassle et al., 1983). A diagram representing this overlap and integration is shown in figure 1. The size of the receptive fields is known to increase with distance from the center of the retina (Daniel & Whitterage, 1961; Perry et al., 1984; Tootell et al., 1982; Weiman & Chakain, 1979). This is due to a decrease in the density of photoreceptors, and an increase in the convergence of photoreceptors to ganglion output elements in the periphery. The larger receptive fields result in lower visual acuity (Rolls & Cowey, 1970). An advantage to a visual system of a resolution that decreases with eccentricity is a reduction in computational demand of the low-resolution peripheral input. The peripheral input can be used for target detection while the high-resolution central vision can be used for target analysis. Since there is only one high-resolution portion of the receptor surface, once a target is located, ambiguity is resolved in the designation of the target and in the separation of foreground from background.

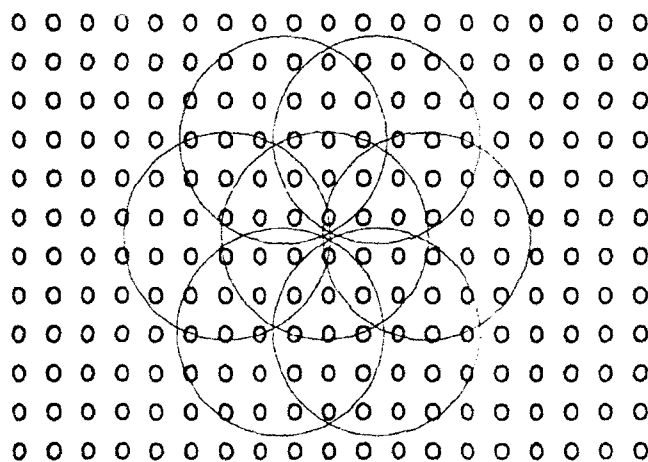


Figure 1. Receptive fields of seven representative output elements overlaid on a local region of the receptor matrix. Receptors that fall within the larger receptive fields of several output elements are connected to each of the output elements.

CYTOARCHITECTURE OF THE VERTEBRATE RETINA

The cytoarchitecture of the outer layers of the vertebrate retina is fairly well understood (Dowling, 1987; Sterling, 1983). The local contrast is computed in the outer three layers of processing elements, including photoreceptors, horizontal cells, and bipolar cells. Photoreceptors make contact with other photoreceptors, horizontal cells and bipolar cells. The horizontal cells make contact with other horizontal cells and with the bipolar cells in a synaptic triad with the photoreceptors.

The receptors transduce light to analog potentials that are distributed to the other layers. Horizontal cells spatially and temporally integrate the receptor activity, distributing it horizontally over a local region of the retina through horizontal to horizontal cell electrical synapses. The bipolar cells are known to be of two types. One computes the difference between the photoreceptor and the nearest horizontal, and the other takes the negative difference. One bipolar cell thus represents the light "on" response of the photoreceptor and the other represents the light "off" response. An on-center bipolar cell shows a depolarization of its membrane potential when a spot of light is presented to its receptive field center. Evidence for an inhibitory surround is the increase in membrane polarization when the spot of light is moved into an adjacent annular region. Off-center cells behave in the opposite fashion. On-center and off-center bipolars are found as complementary pairs with receptive fields that cover the same region of visual space.

LOG-POLAR MAPPING

The mammalian visual system undergoes a log-polar mapping of the receptor input to the processing stations in the central nervous system (Schwartz, 1980, 1984). The mapping is partly the consequence of the bilateralization of the nervous system, and the dedication of large amounts of neural hardware to the processing of input from the high-density, high-resolution portion of the central receptor surface.

A log-polar transformation that models the biological mapping of the visual input is approximated by figure 2. In a polar mapping, the radial dimension of the image is mapped to one axis of the computational plane, and the angular dimension to the orthogonal axis. The net result of the mapping places the projections from the central region of the receptor surface at the top of the receiving matrix, and from the periphery of the receptor surface - at the bottom of the receiving matrix. This must be modified by a logarithmic transform, however, to incorporate the exponential spacing of receptive field centers with eccentricity. In this way, circles centered on the receptor surface will elicit horizontal lines on the log-polar map (changing the size of the circles simply displaces the line by some offset), and straight lines passing through the center of the image plane will produce pairs of vertical lines on the log-polar map, indicating constant angle from the vertical midline.

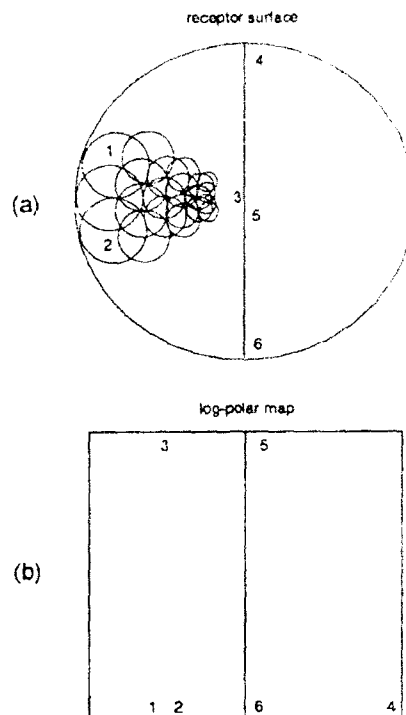


Figure 2. Logarithmic rectangular to polar coordinate mapping of the visual pathway from receptor surface to computational layers. Small circles in (a) represent visual receptive fields; the visual field circles near the center of the receptor surface are omitted in this drawing for clarity. Numbered points in (a) are mapped to correspondingly numbered points in (b).

MODEL

A log-polar mapping from the receptor surface to computational planes that will provide additional visual processes is accomplished in the present model with the following algorithm: (1) increase the size of the receptive fields with eccentricity. While receptor density in the artificial visual system will remain constant with eccentricity (due to the uniform distribution of pixels over the receptor surface), the convergence of the receptors to decreasing numbers of output elements can increase with eccentricity. In the present model, the numbers of output elements lying on any circumference are kept the same. Because of a finite packing density of pixels in the central region, there must be a divergence of receptors to output elements (one to many) to maintain a consistent number of output elements per row of the computational plane, while in the periphery, the mapping is many to one. (2) Divide the receptor surface down the vertical midline from the top of the receptor surface to the center. (3) While rotating counterclockwise, sample the output elements on each circumference from the circumference closest to the center. Then move outward to the periphery as each circumference is completely sampled. (4) Save the sampled output element potentials in a rectangular array by filling the array from left to right and from top to bottom. Form a new row with each new circumference.

Our receptor matrix is an N by N rectangular field, indexed by x and y , compatible with the output of a video frame grabber. The receptive fields, which are composed of groups of neighboring receptors, are mapped to smaller n by m rectangular matrices, indexed by i and j , that make up the computational layers. The index i tracks distance along a radius from the center of the receptor matrix (eccentricity) while the index j tracks counterclockwise rotation from the vertical midline. The mapping is computed once and stored in a look-up table. In the present examples, we use $N = 256$, and set $n = m = 64$, though many other combinations are possible. Larger values of n and m for a given N by N input field improve resolution in the periphery but waste processing of central representations.

The computational layers in this implementation model activities of the retinal horizontal and bipolar cells. The log-polar map from receptor layer to horizontal and bipolar layers is used here for the computational convenience that a rectangular matrix provides. However, immediate neighborhood relationships are preserved in the log-polar map. The output is then in a form that can be further mapped without additional geometrical transforms to computational layers that emulate central processing in such brain regions as the thalamus, superior colliculus, and visual cortex.

The eccentricity (E) of a receptive field, defined as the location of the field center relative to the center of the visual field, varies exponentially with the serial position from the center along the radius of the visual field as

$$E = \exp(\zeta * (i/n)), \quad [1]$$

where i is the serial distance on a radius from the visual field center (from 1 to n), n defines the number of receptive fields to be located on a radius from the visual field center, and $\zeta = \log(N/2)$ with $N/2$ representing the number of receptors (or pixel elements) available along the visual field radius.

The x,y locations of the receptive field centers on the receptor matrix are determined by

$$\begin{aligned} x &= (N/2) - E_{x,y} * \sin \Theta \\ y &= (N/2) + E_{x,y} * \cos \Theta, \end{aligned} \quad [2]$$

where Θ is incremented from $\pi/2$ to $5\pi/2$ by $2\pi/m$. The locations of receptive field centers from one eccentricity to the next is staggered by π/m so that a slightly asymmetric hexagonal matrix of receptive field centers results.

The mapping from the receptor coordinate system to the horizontal and bipolar coordinate system is accomplished by assigning x,y to i,j as n and Θ are traversed above.

The radius of the receptor fields (RFr) is given by

$$RFr = \gamma * E, \quad [3]$$

where F is the eccentricity of the receptive field center (given in [1]), and γ is a constant computed as $(2*(1-\cos(2*\pi/m)))^{1/2}$ to insure that for m number of receptive fields to be defined for any given eccentricity, the radius of each receptive field reaches the center of the next receptive field on the circumference.

The artificial retina is organized in three layers for computation of center-surround receptive fields. The vertical organization of a small representative region of the outer three layers is given in figure 3. An earlier version of this algorithm that did not incorporate the log-polar mapping of the visual pathway was presented in Blackburn and Nguyen (1989).

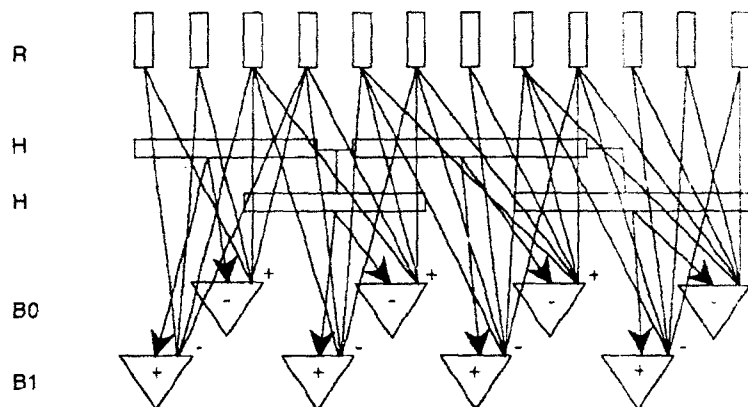


Figure 3. Vertical organization of the outer three layers of the artificial retina. The lines passing from the receptors (R) to the bipolar elements (B0 and B1) through the middle layer of horizontal elements (H) make contact with those elements. Pathways from horizontal elements to pairs of bipolar elements are indicated with arrows and the sign of the influence: excitation (+), inhibition (-). Horizontals have two-way connections with their nearest neighbors.

The algorithm for the integration of receptive field potentials is recurrent and potentials persist over time. All calculations are analog, similar to the graded potentials of the comparable layers in the vertebrate retina.

Horizontal elements share potentials by summing through a buffer a fraction of the potentials from the nearest neighbors and comparing that sum to the current local potential. If the potential on the neighbor is greater, the local potential is incremented; if the neighbor's potential is less, the local potential is decremented. At the same time, the horizontal element looks at the potential on its local neighborhood of photoreceptors and adjusts (up or down) its local potential in an attempt to match the photoreceptor potentials. The horizontal input (Hb) is given by

$$Hb_{ij} = K_1 * \sum_{h,h} (R_{x \pm h, y \pm h} - H_{ij}) + (K_2/6) * \sum_{k,l} (H_{i \pm k, j \pm l} - H_{ij}), \quad [4]$$

where R is the receptor potential, H is the equilibrated horizontal potential from the previous time step, k and l define the six nearest neighbors, x and y locate the receptive field center, and h ranges from 0 to the receptive field radius (RFr , given in [3]) for the particular eccentricity over which the horizontal element integrates receptor output. K_1 and K_2 are constants; in the present examples $K_1 = 0.5$ and $K_2 = 0.2$.

In one time step (t), the potential on H equilibrates

$$H_{ij}(t) = H_{ij}(t-1) + Hb_{ij}(t-1). \quad [5]$$

The photoreceptor potentials in the present model are not changed by the activity on the local horizontal element, but respond only to the external environment.

The bipolar elements then take the difference between the overlying photoreceptors and the nearest horizontal element. In one case, the bipolar elements pass the excess of the horizontal activity over the receptor average; while in the other case, the bipolar elements pass the excess of the receptor activity over the horizontal. Bipolar elements do not pass negative potentials (they are half-wave rectified).

On-center bipolar activity ($B0$) is the greater of the receptor potentials over the equilibrated local horizontal.

$$B0_{ij} = \max \{0, \sum_{h,h} (R_{x \pm h, y \pm h} - H_{ij})\}. \quad [6]$$

Off-center bipolar activity ($B1$) is the greater of the equilibrated local horizontal over the receptor potentials.

$$B1_{ij} = \max \{0, \sum_{RFr, RFr} (H_{ij} - R_{x \pm RFr, y \pm RFr})\}. \quad [7]$$

BEHAVIOR OF THE MODEL

The model was numerically tested on a digital computer. The convergence of receptors upon horizontal elements in the model with the dimensions given for equation [1] is similar to that shown in figure 1 for a region located about 16% of the radial distance from the receptor field center. As can be seen from figure 1, a spot of light or dark in the paracentral region will always activate the receptive fields of at least 3 output elements. The effects of the spot will propagate within the horizontal layer and may result in the activation of neighboring bipolars of opposite direction of contrast sensitivity. That is, a localized spot of light will activate neighboring off-center bipolars as well as the underlying on-center bipolar, and a localized absence of light will activate neighboring on-center bipolars in addition to the underlying off-center bipolar.

The coactivation of on-center and off-center bipolars is shown in figure 4. A 3-pixel diameter spot of light was projected to the paracentral receptor field. The receptive field diameter in the neighborhood of the spot of light was 5 pixels. Because the on-center and off-center bipolars exist as complementary pairs sharing the exact same receptive fields, the level of activation of an off-center bipolar indicates the net inhibition that is present on its complementary on-center bipolar. The surround field can be reconstructed for a particular stimulus condition by considering the activations of both on-center and off-center elements in the neighborhood.

Figure 5 shows the responses of on-center and off-center bipolars produced by a 3 pixel-wide line radiating out from the center of the receptor surface. The receptive field sizes represented range from diameters of 4 pixels at the top of the matrix to 10 pixels at the bottom. Note that there are several shapes for the receptive fields within rows of figure 5.

on-center										off-center																		
e	f	g	h	i	j	k	l	m	n	o	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s
0	0	0	0	0	0	0					0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0				0	0	0	1	4	4	1	0	0									
0	0	0	0	0	0	0					0	0	0	2	14	2	14	2	0	0								
	0	0	13	13	0	0					0	0	2	23	0	0	23	2	0									
0	0		37	57	37	0					0	0	1	16	0	0	0	16	1	0								
	0	0	7	7	0	0					0	0	4	7	0	0	7	4	0									
0	0	0	0	0	0	0					0	0	0	4	12	18	12	4	0	0								
	0	0	0	0	0	0	0				0	0	0	1	1	1	1	0	0									
0	0	0	0	0	0	0					0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Figure 4. On-center and off-center bipolar element activity in response to a stationary bright spot of 3 pixels in diameter. The spot fell on the center of a receptive field with an excitatory center diameter of 5 pixels. Local neighborhood relationships are maintained in this log-polar transformed map. The column index shows the complementarity of on-center and off-center bipolars.

Symmetry in center-surround receptive fields has been described for biological systems (Hubel & Wiesel, 1962). Even-symmetry is defined by a center with an equally weighted surround of opposite effect. Odd-symmetry is defined by a receptive field that contains only two regions with opposing effects, separated by an edge or non-encompassing border. Symmetry in receptive fields of the current model emerges from a rather uniform spread of potentials to neighboring horizontals. Even-symmetry is expected by the pattern of connections, but odd-symmetry can also arise under dynamic conditions. The persistence of activity in the horizontal elements will contribute to the appearance of an odd-symmetry in the receptive field with a moving bar because the rate of exchange of activity between the horizontals lags the rate of change of activity from receptors to horizontals. Figure 6 shows potentials resulting from a rotating bright radial line of 1 pixel in width on the receptor surface. The line moves across the bipolar map from right to left and leaves a trail of inhibition behind.

on-center								off-center																							
i	j	k	l	m	n	o	p	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t	u	v	w	x
0	0	133		0				0	1	1	5	56	44	0	44	56	5	1	1												
	0	39	39	0				0	1	1	10	100	0	0	100	10	1	1	0												
0	0	139		0				0	1	1	3	35	20	0	20	35	3	1	1												
	0	48	48	0				0	1	1	9	96	0	0	96	9	1	1	0												
0	0	98		0				0	1	1	4	40	29	0	29	40	4	1	1												
	0	40	40	0				0	1	2	16	38	0	0	38	16	2	1	0												
0	12	61	12					0	1	1	4	43	0	0	0	43	4	1	1												
	0	60	60	0				0	1	1	8	82	0	0	82	8	1	1	0												
0	0	100		0				0	1	1	2	20	60	0	60	20	2	1	1												
	0	18	18	0				0	1	1	5	56	0	0	56	5	1	1	0												
0	0	71		0				0	0	1	2	22	1	0	1	22	2	1	0												
	0	35	35	0				0	1	1	5	53	0	0	53	5	1	1	0												
0	0	53		0				0	0	1	2	15	43	0	43	15	2	1	0												
	0	37	37	0				0	1	1	4	48	0	0	48	4	1	1	0												
0	0	47		0				0	0	1	2	18	11	0	11	18	2	1	0												
	0	38	38	0				0	1	1	4	46	0	0	46	4	1	1	0												
0	0	39		0				0	1	1	13	26	0	26	13	1	1	0													

Figure 5. On-center and off-center bipolar element activity in response to a stationary horizontal bright line of 3 pixels in width radiating out from the center of the receptor matrix. Eccentricity of element location increases from top to bottom of the figure. Local neighborhood relationships are maintained in this log-polar transformed map so that the effects of the line appear vertically.

The partial overlap of receptor convergence to horizontal elements and the horizontal spread of adaptation activity in the horizontal layer with time delays creates the

conditions for the center-surround receptive fields. A homogeneously active receptor surface is eventually matched by locally uniform potentials in the horizontal layer. This eliminates the differences in activities between on-center and off-center bipolar cells. With eccentricity, the convergence of receptors to horizontals increases so that receptive fields become larger, but the degree of overlap of the receptive fields relative to the size of the fields of horizontals remains somewhat constant.

DISCUSSION

The current neural doctrine holds that natural neural systems compute at chemical synapses by adding and subtracting the effects of -- or modulating the transmission of -- quantities across the synapse (Kandel et al., 1991). In modeling these pre- and post-synaptic mechanisms, producing the required behavior by simple processes of addition, subtraction, facilitation or inhibition might also be useful. However, this low level of computation is often forsaken for more abstract descriptions of the neural processing.

on-center														off-center													
a	b	c	d	e	f	g	h	i	j	k	l	m	n	a	b	c	d	e	f	g	h	i	j	k	l	m	n
0	71	0	0	0	0	0	0	0						3	0	0	204	71	22	8							
34	71	0	0	0	0	0	0	0						0	0	181	144	41	12	5							
0	103	0	0	0	0	0	0	0						7	0	0	175	65	20	8							
0	76	0	0	0	0	0	0	0						19	0	256	109	34	12	5							
0	75	12	0	0	0	0	0	0						2	0	0	145	57	19	8							
51	63	0	0	0	0	0	0	0						0	0	196	94	31	11	5							
0	59	28	0	0	0	0	0	0						8	0	0	113	43	14	6							
0	40	0	0	0	0	0	0	0						23	0	181	66	20	8	4							
0	57	16	0	0	0	0	0	0						4	0	0	109	32	11	5							
3	34	0	0	0	0	0	0	0						0	0	69	52	17	7	3							
0	29	10	0	0	0	0	0	0						6	0	0	91	30	10	4							
0	37	0	0	0	0	0	0	0						13	0	83	52	17	7	3							
0	30	2	0	0	0	0	0	0						3	0	0	77	27	10	4							
0	31	0	0	0	0	0	0	0						9	0	68	41	14	6	3							
0	34	9	0	0	0	0	0	0						2	0	0	57	20	8	4							
0	27	0	0	0	0	0	0	0						9	0	90	32	12	5	3							
0	30	5	0	0	0	0	0	0						3	0	0	47	18	7	3							
0	21	0	0	0	0	0	0	0						9	0	78	30	10	5	3							
0	24	6	0	0	0	0	0	0						3	0	0	52	17	6	3							
5	14	0	0	0	0	0	0	0						0	0	41	26	9	4	2							

Figure 6. Odd-symmetry of on-center and off-center bipolar element activity in response to a radial bright line of 1 pixel in width moving from right to left across the map.

While mathematical formalisms employed in the abstract descriptions can achieve adequate prediction or approximation of neural system behavior, they often assume operations that have not been observed in the mechanisms of the neural systems in question (e.g., exponentiation, division, and trigonometric operations). However, the use of formal abstractions has not been of great concern to neural modelers, perhaps because of the realization that all abstract mathematical functions can be approximated by integration or differencing of finite quantities. It is, after all, through such reduced algorithms that the formal descriptions are demonstrated on digital computers. Yet, even the computer programmer/modeler is, in many cases, isolated technically from the low-level computer operations through the use of pre-coded functions, and may never have to know how those functions are implemented. Thus the use of abstract formalisms in neural modeling possibly can obscure or even impede the discovery of the computational mechanisms employed by the natural neural systems. On the other hand, the use of elementary operations to model neural processing may provide additional insight into the neural mechanisms and their consequences.

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